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Forest dynamics: a broad view of the evolution of the topic, including some recent regional contributions

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Abstract

During the last two centuries, social perception of forest roles has suffered deep changes. New environmental roles, i.e. CO_2 storage and biodiversity, have been added to erosion control and watershed regulation. These changes require new knowledge and tools to develop a new understanding of forest dynamics. Some come from studies on past vegetation responses to climate changes. I recall here some old ideas on plant communities and their dynamics in ecology and forestry and the trend to use quantitative and modelling approaches under a new community concept based on environmental constraints, life-histories of available species and disturbances. New succession mechanisms have been added to the Clementsian facilitation, legacy after disturbance is now considered essential and succession has been described as a cycle by including the phases of community decline and resources and space liberation. I summarize some ideas related to Mediterranean ecosystems and to the relation between forest dynamics and global change and I review some main types of models used in forest dynamics studies. Finally, I consider fire ecology and some advances made in our institute on this topic.

Key words: Forest roles, succession, disturbance, forest models, global change, autosuccession, forest fires.

Resumen

Dinámica forestal: una visión general de la evolución del tema, incluyendo algunos desarrollos regionales recientes

Durante los dos últimos siglos, la percepción social del papel del bosque ha sufrido cambios profundos, que incluyen el reconocimiento de nuevas funciones en relación con el almacenamiento de CO_2, la biodiversidad, etc. Estos cambios requieren nuevos conocimientos y herramientas para desarrollar una nueva comprensión de la dinámica forestal. Parte nos los aportan los estudios de respuestas pasadas de la vegetación a los cambios climáticos, que han ayudado a erigir un nuevo concepto de las comunidades vegetales. Discuto aquí viejas ideas de ecología y silvicultura y el aumento de las aproximaciones cuantitativas y el uso de modelos y un concepto de comunidad basado en constricciones ambientales, historias de vida de las especies disponibles y perturbaciones. Se han añadido nuevos mecanismos a la facilitación clementsiana. Las sucesiones pueden describirse como ciclos y el legado tras la perturbación es esencial para la sucesión, Resumo algunas ideas nuevas sobre las sucesiones en ecosistemas mediterráneos y sobre la relación entre dinámica forestal y cambio global y reviso algunos tipos básicos de modelos empleados en estudios de dinámica forestal. Finalmente, considero la ecología del fuego y algunos avances realizados sobre este tema en nuestro centro.

Palabras clave: Funciones de los bosques, sucesión, perturbación, modelos forestales, cambio global, autosucesión, incendios forestales.

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Introduction

People have always been provided by forests with a number of direct services, like products used as food or building materials, as papers or fibres, or they have used them as refuges against enemies. Also, they have received indirect benefits, like water runoff regulation or forest influence on global climate. At the same time, forests have been always cleared to gain soil for crops or grasslands or to avoid their use as refuges for other people or wildlife considered dangerous. Early in our history, Plato mentioned some negative effects of deforestation, especially soil erosion. A generally accepted conception was that forests could be treated simply as a source of products to be extracted, or as something to be removed in order to promote crops and progress. This was a consequence of a misunderstanding of the benefits that forests were giving to people. Deforestation affected very large surfaces and was a direct result of the settlement and demographic increase of human societies and timber or coal production. The influence of man action on forests was so evident that for centuries people thought that it was the only cause of forest change. This was another misconception. Forests change by themselves and as a result of environmental changes, climate for instance. Some changes occur in relatively short times (years, decades), other need millennia and escape to direct observation by people.

During the last two centuries, and especially during the last decades, the social perception of forest role has evolved. Whereas a part of the society has continued to see the forests mainly as a resource or an obstacle, an increasing proportion of people, mostly urban people, appreciate the recreational opportunities and the aesthetical values offered by the forests and their role as wildlife habitat. Scientists, that discovered much time ago the relevance of forests in erosion control and watershed regulation, claim now that forests and their soils are major storages of carbon and that gas exchanges of forests have a large influence on the atmospheric composition and then on the global and local climates, which depend on forest characteristics and composition. The increasing importance of recreational uses of forests, and their understanding as biodiversity refuges and carbon storages, requires new forms of management, looking for increasing sustainability. This means that forest management must change toward maintaining forests in a more natural condition, while still utilizing their resources. And this change requires new knowledge and tools to develop a new understanding of vegetation dynamics.

We know that climate and vegetation have changed over the millennia, and that both are mutually dependent. Pollen records reveal past vegetation changes (Davis, 1983; COHMAP, 1988). Climate is affected by CO_2 concentration in the atmosphere and vegetation is a major factor in CO_2 budget of continental ecosystems. Fast changes are occurring now, as a result of forest clearing in the tropics and some Mediterranean areas, forest decay due to pollution, and forest losses due to intensive logging in temperate and boreal forests, changes in fire regime, fragmentation and elimination of primeval or old forest remnants, changes in the atmospheric composition and the climate due to human activities, etc. All these changes affect forest function and the biological diversity they contain.

Forests are complex and very diverse systems. In despite of increasingly large and expensive research efforts, many aspects of their function are unknown. It is uttermost difficult to understand the precise mechanisms involved in trees and forest responses to environmental changes. Nevertheless, when the immense importance of forest functions is considered, it is clear that we need to implement management procedures that will protect them and their sustainable use. We need to know their present state, the effects of our actions and the spontaneous trends of response under a number of future environmental scenarios, in order to make projections to the future. Through most ecological history, changes in forests, vegetation or ecosystems have been approached from an observational and qualitative, informal point of view. This has produced a number of untestable general theories that reached a large influence on ecological thinking and practice. Let us to review briefly the main changes occurred in the theory of vegetation dynamics.

Old ideas about vegetation dynamics

Many advances in the theory of vegetation dynamics are related to forest modelling. We will use here the following large and comprehensive definition: forest dynamics is constituted by the processes of change in the composition, structure and function of forests. This

includes processes that occur at very different scales of time and space. There are two main historical backgrounds for forest dynamics. One is the study of ecological succession. Initiated in the early XXth century, it reached a first theoretical assessment with Clements work *Plant succession* (1917). Clements theory gained much acceptation as a new paradigm, but was questioned from its beginnings by Gleason (1917, 1939). In Clements view, succession is a gradual, directional, autoorganized change from pioneer to stable, mature community states that, when reached, will remain unchanged. This view was modified in many details, but in its basic aspects was still in use by botanists and terrestrial ecologists by 1970-80. Even as late as 1969, E.P. Odum stated that succession is «an orderly process of community development that is reasonably directional and, therefore, predictable» and that succession «culminates in a stabilized ecosystem» (Odum, 1969), a conception that is essentially the same that Clements one. The alternative individualistic ideas about plant communities in Gleason's tradition, that is, every plant species behaves on its own, responding to its specific requirements, were reinforced by the development of plant demography but not became generally accepted until, by 1980, when a reductionist point of view, axed on demography and ecophysiology, gained a dominant position in ecology and when Davis (1983) demonstrated that glacial and interglacial events produced changes in the distribution of tree species with rates that were specific for each one species and not global community migrations. This destroyed the old clementsian idea of a plant community as a quasi-organism, with young, developing and mature states following an ordered, directional process.

The second historical background comes from forestry. The essence of scientific forestry is to manage forests evolution in order to reach the appropriate composition and structure that will maximize some benefits like wood or other productions, protection against erosion, watershed's regulation, etc. Most forestry efforts have been directed to evaluate the capability of land to produce timber and to ameliorate this capacity by forest management. All these activities have a longer history than the science of ecology: the foundations of scientific forestry were settled during the XVIIIth century, mostly in Germany. Foresters have added their views to ecological theories of forest dynamics along the XXth, in particular after the remarkable contributions by Watt (1947). Forest science has been always regarded as a statistical science, because it studies populations of individuals with a too much long life span to be followed by an observer, thus it requires models to predict the processes of tree growth, ageing and mortality, the consequences of forest management, the effects of disturbances and the environmental changes associated to growth, disturbances or mortality. Quantitative models were easier to develop for calculating growth and economical balance of regular evenaged plantations. Successional hypothesis were quite simple, and based on parameters like birth and death rates, growth rate, effects of competition for space, light, water and, some times, soil nutrients.

Early forest models were too simple to the ecologist mind, because most natural ecosystems are composed by unevenaged, irregular populations of many species, heterogeneously distributed on space. Modellisation of natural forest ecosystems is a difficult task, but a number of attempts more or less successful have been based on different approaches, at individual, plot or larger scales. Bottom-up mechanistic models proceed from recruitment and death of individual trees or from leaf gases, water and nutrient exchanges, to the entire structure and function of the canopy or forest. Up-down models are being used to determine environmental and geographical constraints and the possibilities have greatly increased due to the availability of remote sensing data and geographical information systems (GIS). We will discuss models later in this paper, but we can not forget that advances in modelling depend on advances in theoretical understanding.

Present conceptions on forest dynamics

As a result of theoretical discussion, the progress in ecological understanding and the joint work of ecologists and foresters, the paradigm of forest dynamics has changed during the last quart of a century. Now, natural communities are view as the result of environmental constraints, life-histories of available species, and disturbances that can be periodic or aperiodic, small or catastrophic, programmed (as treatments in forest management) or stochastic (as wild fires, hurricanes, etc.). This is entirely different from a simple directional autoorganized process, comparable

to the growth of an organism, as stated by Clements succession. The refusal of this theory based on emergent properties of populations and communities has needed many years and a number of steps. For example, Egler (1954) sustained that nearly all the species are present from the beginnings in the community (theory of initial composition), and that the succession is the result of a sequential expression of this presence, due to different rates of growth and different final size. Peet and Christensen (1980) considered that succession is a consequence of the variation in reproduction, settling, growth and mortality, introducing a demographic point of view that is particularly useful if the aim is to produce models. Huston and Smith (1987) described the succession as a change in relative abundances of the dominant species. A consequence of the demographic emphasis was the gap theory. A gap is the hole produced in a canopy by the fall of a dominant tree. Gap dynamics is advantageous for modelling, but describes only a part of forest dynamics, excluding primary or secondary (following a large disturbance) successions. It has been applied successfully to some boreal and tropical forests, but it is more difficult to apply to irregular, unevenaged and mixed Mediterranean forests, with a large history of exploitation.

Another point where the approach has changed is about successional mechanisms. The mechanism recognized by Clements, facilitation of the next step by the previous one exists and works, but it is not the only mechanism explaining successions. Connell and Slatyer (1977) proposed two more, tolerance and inhibition by the pioneer plants of mature stages plants, as explained in all the ecological textbooks published from then.

Clements conceived succession as a progressive construction of the community to a final stationary climax state. This is a clearly incomplete view. There is no final, mature climax: forests at first grow fast, then slow, nutrients become increasingly linked to organic structures and less available, so limiting production (the role of phosphate in this sense seems especially relevant in very different biomes, see Wardle *et al.,* 2004) whereas respiration continues to increase. The accumulation of old trees and decomposing wood will then increase the danger of a sudden pest or fire breakdown that liberates energy, nutrients and space. Then, the process of regrowth can begin from seeds or resprouts. The sequence is not predetermined: random factors, like season or intensity of the disturbance, will be very important. So, the forest succession is not a linear process of growth, but a more or less cyclical chain of states. Hölling (1988) has defined a sequence that includes establishment of seedlings, self-thinning, opening gaps by dominant trees mortality, development of a mosaic including patches in every one of all these phases, decay and reinitiation. Clements considered essentially a step of exploitation (fast colonization of disturbed areas) and a step of conservation (the slow process of accumulating energy and matter, with mortality depending mostly on competition), whereas Hölling cycles include two new steps, liberation (an equivalent to the creative destruction described by Schumpeter for economy), when nutrients are suddenly available as a result of the destruction of biomass (by a wild fire, a pest or other causes); and reorganization, where edaphic processes attenuate nutrient losses and make nutrients available for a further exploitation phase. Cyclic Hölling model is, essentially, a reelaboration of Watt (1947) on forest cycles.

We can conclude, from this broad discussion, that the Clementsian paradigm for succession has been abandoned. Ecologists now insist in the importance of the *legacy,* as seeds, structures, available resources, surviving animals, etc., after the disturbance; the seed's arrival rate, that will determine colonization and depends on seed's production and dispersal within or around the disturbed area, and the abundance of vector animals; the survival rates of seeds and seedlings, depending on environmental variables and predation; physical changes in the milieu; competition, inhibition by other plants due to chemical interactions, presence or lack of micorrhyzic fungi, etc. As a result, the end of a secondary succession is not predefined by the climate (as in climax theory). The process can follow different trajectories and reach different mature states that can not be considered as ending stable points because the process is cyclic. These new ideas make easier to approach ecological theory and practical forestry, because there is a common interest in processes at individual, plot or population levels. Prediction is strictly impossible, but quantitative models can be built to explore possible developments under different scenarios and to generate projections. At larger scales, as those of landscape and region, a more traditional community approach can still be useful to do some broad predictions.

Autosuccession

For some Mediterranean ecosystems, Californian chaparral, Hanes (1971), and garrigue (Trabaud and Lépart 1980) found evidences that secondary succession involved few changes in specific composition after a fire, because the preexisting species were able to conserve their spaces by fast resprouting from fire-resistant structures or by fire-stimulated seed germination. Hanes described this process as autosuccession. Recent work on after-fire regeneration in the Mediterranean Basin indicate that this is not at all a general case for every Mediterranean ecosystem, and for every Mediterranean species, and a large number of exceptions have been described. An study by Rodrigo *et al.* (2005) demonstrate that, in general, *Quercus* species (resprouters) and the pines *Pinus halepensis* and *P. pinaster* (serotinous seeders that produce abundant seedlings) showed direct regeneration patterns (autosuccession), whereas, in contrast, forests of *P. nigra, P. sylvestris* and *P. pinea* (non-serotinous seeders that produce few seedlings) changed to other states after fire.

This means that managers might not be take for sure that Mediterranean vegetation is fire adapted and will regrowth without changes after a short time. Local conditions, fire legacy, specific biology of available plants, time of fire occurrence, fire severity, fire intensity or fire size, etc., will have a significant effect, and managers have to analyze all these factors before taking decisions about things to do after the disturbance. Changes in disturbance regimes will also modify plant responses.

Forest dynamics and global change

A new challenge has appeared during the last decades for ecologists and foresters, with the concern about global change. Far-reaching effects can be expected to result from global change on forests. Global change has a number of components, like the change in atmospheric composition (that includes the increase in CO_2, in some cases acting as a fertilizer, the increase in tropospheric ozone or in UV radiation, that have negative effects on plants, etc.); the climate change (in temperature, rainfall, water balance, frequency of extreme events, fire regime, etc.); the change in land uses (forests can be substituted for grasslands or agriculture and viceversa); biological invasions (by plant, animal or microbial pests); economic globalization (changing demands on forest products); etc. The consequences of all these changes on forests will affect their composition, structure and function, and so they will affect, too, all the forest services to mankind, as the amount and distribution of water supply from watersheds, erosion control, wood, fibre, fruits, fungi, hunting or cork production, biodiversity, landscape and recreation, and feed-back atmospheric and climate changes. Plant and soil forests sequester most of the terrestrial biosphere's carbon, or liberate it when forests are burnt or cleared. Changes in all these issues will modify the role of forests as key components of the global carbon cycle and as key contributors of biological feedbacks to global climatic change. Forest fires and deforestation will accelerate atmospheric and climate changes. Afforestation has been considered a possible compensation for CO_2 emissions in the United Nations Framework Convention on Climate Change (UNFCCC) and the Kyoto Protocol, but many people objected to this, even from a conservationist position, because mature forests are not effective in accumulating carbon and new tree plantations can cause heavy disruptions of soils, liberating carbon to the atmosphere at the beginning and also again at the end of the production cycle. In any case, mature forests might be protected, because they store large amounts of carbon. Too simplistic assumptions about forest role in mitigating climate change can induce the development of bad practices (i.e. new plantations on grasslands). Our knowledge of stocks and flows during forest growth or in wood products life is far from exhaustive. Carbon budgets for all main forest types are needed at nation scale, and they are also needed for any tree plantation made with the purpose of mitigating CO_2 increase. Additional obvious needs are the modification of traditional forest inventories to account for carbon storage and to permit carbon storage monitoring and the development of new and better models for gas exchanges and budgets.

How to analyse forest responses to changes?

If we want to assess the responses of forests in front of changes in the environment, it would seem that the

easier way is to monitorize a number of variables for a period of time, observing these variables whereas some known changes occur (for instance, in atmospheric composition, average temperature, etc.). Measuring, and adequately marking, a set of permanent plots permits to follow changes in composition and structure. This has been done in some cases with a few plots that have been monitorized for decades. Now, there is a trend in forest inventories to leave some permanent signal in order to found the same plots in the future. The marks on trees vanished in a few years, but the use of GPS and metal pieces buried in the centre of the plot that can be refound with a metal detector can aid to solve this problem. In any case, the look for precise plots involves labour and money cost. Then, even if plots are refound and changes are detected, their causes can be multiple, involving climate, clearings, pollution, pests, etc., and frequently they are not easy to distinguish. Forest inventories can permit to analyze some variables relevant to define the ecological characteristics of the plots, like leaf area index (LAI) or species richness (Terradas *et al.,* 2004). The best possibilities are sets of plots in the limit of areal distribution of a species, where local extinctions or colonizations can be best recognized.

Monitoring of functional variables is much more difficult. Unluckily, many environmental variables, like yearly or seasonal rainfall or temperatures, largely fluctuate on interannual basis, and plant responses, like phenology, fruit production or growth are also very variable. In the field, the method requires very long term observations, measuring instruments and sensors and the interpretation of results will be confuse because to many things occur at the same time. Long-term monitoring is, also, very demanding, not only in time but also in work and in commitment, what explains that only a collection of very few studies of this type is available in the world. The measurement of some variables, for instance those related with gas exchanges like eddy covariance, requires expensive towers and sensors.

One solution is the design of experiments under control. If we create an artificial environment, we can observe ecosystem responses to changes in isolated variables. This sounds nice, but forests are not flies. They are too big, too complex, and their components are too long-living, what means that past can influence future responses in complicated ways. Nevertheless, some experiments have been done since the 1960's with entire watersheds, using different treatments as clearing or pesticide fumigation (the Hubbard Brook Ecosystems Study, Bormann and Likens, 1979 has been pioneer, but see also Waring and Franklin 1979 and some more). In Spain, the studies on holm oak forests at La Castanya and Prades, initiated in 1978, were the early attempts in that direction (Rodà *et al.,* 1998). Other experiments used forest plots or plots on shorter types of vegetation (by modifying the amount of rainfall that reach the soil using covers that can be extended or retired handly or automatically (for instance, the European project Climoor on heathlands, Peñuelas *et al.,* 2004), a net of electric wires to increase soil temperature, etc. Experiments permit to obtain relatively fast results if compared with long-term monitoring, but are also costly, especially in forests, and their interpretation is rather complex because it is not possible to change just a variable at one time in the field. As a result, even if a large array of experiments has been developed in many types of terrestrial ecosystems, patterns of responses described are clearly incomplete in practically all of them.

A third approach is the reconstruction of past changes using paleoecological indicators that can be correlated with climate history, like pollen analysis or dendroecology combined with isotopic datation and chemical analysis of remnants. This has produced a number of interesting studies and results, mostly for the last early postglacial period, concerning vegetation changes with temperature. Occasionally, some evidences can appear on man role or on possible effects of changes in rainfall or fire regimes, but usually the increase of man action during the more recent periods make very difficult the understanding of the observed patterns. Using pollen data from a number of sites, and correlating it with the history of climate, it has been possible in some cases to determine the pathways and rates of migration across the landscape for a number of tree species in response to postglacial climate changes (Davis 1983, Delcourt and Delcourt 1977). A fairly good possibility is to study the tree-lines, where responses to climate changes are especially sensitive (Camarero 1999).

Models

The last possible way to evaluate forest responses to change is the use of ecological theory to produce

computer models and then projections (Botkin, 1989). Computer models can significantly enhance our ability to address the issues of cause and effect relations on long temporal and broad spatial scales.

Obviously, «experiments» with models are easier and much less time and money demanding than field experiments. Models provide a link between research and management, because they can produce projections under different management scenarios and without waiting for actual dynamic processes that can need centuries. Models can be used to extrapolate short-term and small-scale measurements that can be done in the field to long-term and large scale of entire ecosystems (Pacala *et al.,* 1996). The value of the model will depends on its capacity to catch the main aspects of the ecosystem structure and function using the simplest array of variables possible. This is a very important point: the model might not attempt to approach a reproduction of reality, because then it would become as impossible to understand as the reality is. Simple models do not reproduce reality, but can give us a broader schema where sensitivity to some selected variables can be tested, and then the models can have heuristic value.

There are many types of models referring different aspects of vegetation dynamics. We can distinguish two main compartments in a vegetation community, soil and plants. Soil is an essential part of the ecosystem; in most cases it contains more organic matter that plants and animals together. As a result, we need to understand the dynamics of soil organic matter if we want to have acceptable accounts of carbon balance. Processes involved include litter-input, depending on forest productivity and stochastic events (i.e storms, pest attacks) and decomposition (its rate depends on environmental conditions, like temperature and moisture, litter chemical characteristics and soil biota). The balance between both processes changes through succession. Root dynamics is unknown for most ecosystems, a serious lack because underground structures are a substantial, sometimes the most substantial part of total biomass, and because fine-root can have even higher productivity and turnover than leaves. There are specific models of the dynamics of soil organic matter, but few studies have analyzed with some detail flows and storages. The second compartment, plants, is much easier to measure. We summarize here the main types of models of forest dynamics.

Descriptive models. In the classical works by Clements or Gleason vegetation dynamics can exemplify the deterministic (Clements) and stochastic (Gleason) varieties of descriptive models. However, descriptive models are not always just verbal. Statistical techniques have been used in order to describe in a quantitative way the successional changes in the composition of plant communities or in order to discover successional trends in temporal or spatial patterns.

Forest growth models. The classical theory of population dynamics use exponential and logistic models of the growth of a single population and Lotka-Volterra equations for predator-prey interactions. These models are very simplistic, the entire population is described by a single number of individuals and rates of birth and death, without any account for sex or age structure. Reciprocal effects between two species are described by a single parameter, a coefficient of interaction. These models do not include environment and the stochastic events, and all events are continuous and deterministic, not discrete and stochastic. Formally, these models consist in sets of simple, continuous, differential equations that can not fit real data.

Later, new models have been developed, based on the increasing knowledge on ecosystems function. Foresters and ecologists have taken a number of approaches, intended to simulate growth in forests that can be formed by one or more species, evenaged or unevenaged. Some are based on leaves, others on single trees, others on individuals, plots and gaps, but many of them pretend to simulate the entire forest evolution. Some of them describe populations as a number of classes, each one defined by an average individual. Others employ variability in individual sizes but do not consider space distribution of the individuals. There are also spatially explicit models. Main variables in all these models use to be: a) those related to regeneration, as recruitment, resprouting rates, seed production, germination, seedling growth; b) those related to tree growth in high or diameter; c) those related to geometric competition, including spatial interactions that are mostly asymmetric interactions; d) those related to resources competition, including light, water or nutrients; e) those related to death rate.

Single-tree models use dendrometric variables to simulate the growth of an average tree as a response to a stand quality index, and to competition that depends

on the distance to neighbour trees and on the basal diameter of these trees. These models are appropriate to the simulation of evenaged one-species plantations.

Individual based forest models take in account every individual tree in a stand that is usually divided in plots with a grid. Earlier models were applied to evenaged one-species or mixed forests in order to make crop predictions. They refer to data and regressions obtained from the monitoring of permanent plots. With these regressions, and taking in account the stand and species characteristics, they estimate the growth of each tree. Two types of these individual based models have become popular between the ecologists, patch models and gap models.

The main idea in patch and gap models is that the success of tree species depends on light variance (Botkin, 1993a; Botkin *et al.,* 1972; Shugart, 1984; Horn *et al.,* 1989; Urban *et al.,* 1991). In gap models, size and age of individuals are the essential variables. A first procedure determines gap formation, seedling establishment and suppressed trees death. Then, a second procedure calculates environmental changes induced by each tree. Early models of this kind ignore the explicit spatial structure of the mosaics and work on an ideal variance, as in JABOWA-II (Botkin 1993b), a population dynamics model dealing with many species. Space is divided in a grid of unit cells. A dominant tree death creates a gap. All gaps are considered to be regular in size. Diameter at breast height (DBH) and annual increase in volume (calculated at first as a function of LAI) are the main variables. Some simple assumptions are used for the relations between tree variables, environmental variables and resources availability, and competition within cells is included by a decrease in resources availability, mainly nitrogen. In earlier versions of JABOWA, there are three main subroutines that calculate growth of each tree (in a deterministic way) and birth and death (in stochastic ways). Partial differential equations are used to simulate space and time processes occurring in the gaps. Depending on litter abundance, seed predation, seed availability, radiation that reaches the soil and other variables, the model simulates regrowth within the gap. JABOWA uses isolated discrete cells and makes two essential assumptions: dispersal comes from an external list of potential colonists; and recruitment comes from a prefixed external flora. There is no competition or dispersion between cells. The model is conceptually advanced within the array of available succession theories. JABOWA admits that processes can be discrete, integrates stochastic processes as a fundamental part of the dynamics and growth and regeneration are functionally linked to environmental variables.

Recent descendants of JABOWA have included spatial structure and competition and let recruitment to come from present adult trees, as in FORET (Shugart 1984; Shugart and Prentice 1992; Shugart and Smith, 1992), a model that uses discrete cells but permits some communication between neighbours, like internal dispersal (without spatial constrictions). In SORTIE, forest dynamics emerge as the result of local competition for light among the constituent trees. The responses of the trees to their local light and the local dispersal of seedlings are estimated from field data (Pacala *et al.,* 1993; Pacala *et al.* 1996). SORTIE is both individually based and spatially explicit. Both competition and dispersal are estimated continuous functions.

The «gap models» have been used to simulate long-term dynamics of a wide range of forest ecosystems on several continents under current climate (Shugart 1984). Some models have been adapted to European conditions, like FORECE (Kienast 1987) and FORCLIM (Bugmann 1994), used to simulate forest dynamics in the European Alps, and FORSKA (Leemans and Prentice 1989; Prentice *et al.,* 1993), a model for Sweden forests.

Stand models. There are very old models that employ production tables and quality of stands and are able to simulate statistical distributions of DBH. Modern stand models use ecophysiological processes and biogeochemical cycles, hydrological flows, etc. to determine tree growth. Perhaps the father of this kind of models is FOREST (Ek and Monserud 1974). It begins with a state of the stand defined by vertical and horizontal structure and with some data on reproduction, growth, mortality and competition. Seed production and dispersion, and seedling growth and competition are very important to define recruitment on free land. These models are static, with trees fixed in space and time, but have been ameliorated in a number of ways.

Many models simulate energy and matter flows by dividing the ecosystem in compartments (leaves, bark, stems, litter, etc.). Inputs can be temperature, rainfall or intercepted photosynthetically active radiation (PAR). Canopy models use LAI and its seasonal change as a

main variable. Leaf models make PAR a variable affecting photosynthesis and transpiration. A model of this kind developed in Spain is GOTILWA (Growth of Trees is Limited by Water) (Gracia *et al.,* 1999), a process model based on monospecific stands that uses climatic variables, plot or watershed variables and tree variables and functions. Forests are divided in size classes with individuals assumed to be identicals in each class. Spatial distribution is not considered. Subroutines include leaf-level processes and canopy and litter processes. Designed for Mediterranean forests, it has been used successfully in other European forest types and is all times being ameliorated.

Some process models evolved from FOREST are specifically directed to link remote sensing data with vegetation dynamics. For instance, BIOME.BGC (Running and Hunt, 1993) is very sensitive to LAI and simulates a number of physiological processes (photosynthesis, respiration, evapotranspiration, decomposition, N mineralization). Normal difference vegetation index (NDVI) data can be used for comparison.

Ecological models based on population dynamics or individuals

They are founded in rates of change of the number of individuals of one species or in the productivity of one or few species. Usually, they consider life-forms or life-story attributes (i.e. Noble and Slatyer 1980). Huston and Smith (1987) criticized population models applied to succession because interactions occur at the individual level, and individuals are different in their size, age, physiological state or environmental conditions that affect them. They proposed to modify JABOWA or FOREST type models making growth rates to be determinants for relative abundances.

Markovian models. These models are based in the definition of a number of ecosystem states and in the construction of a transition matrix between all pairs of states. The matrix is made of transition probabilities (Horn 1975) within each pair of states, with values depending only of the present state of the system and not of its previous history. The result is a distribution of frequencies of the possible states that is independent from the initial one, and the system evolves on a probabilistic way until the most probable end state. The states can be defined by dominant species or other criteria. The transition probabilities can be obtained from series of observational data or comparisons between a chronosequence of aerial photographs or maps. The rates of transition can also be estimated by similar ways. A main objection is that transition probabilities are not stationary and can change in time and space. There are other problems, because history can effectively influence transitions through more than one step and because sampling presents autocorrelation effects. Nevertheless, Markovian models are simple to use and very popular in landscape scale approaches.

Cellular automata and disturbance models. If we divide the study area in cells using a grid and one state is recognized to each cell, we can define some rules for the occurrence and propagation of a disturbance (i.e. a forest fire) to the neighbour cells. Other disturbance models are based on the rate of advance in function of the slope, climatic variables, available fuel, etc.

Landscape models. They are based in the use of some of the previous techniques. If there is no account for the interaction between patches structure and dynamics, then Markovian models or gap models can be used on the basis of GIS. If the interaction is considered, a preferred approach is based on gap models and cellular automata: biomass dynamics in each cell unit modify the establishment, growth and mortality in neighbour cells.

Combined or integrated models. Different models can be combined by a nesting procedure, with more detailed mechanistic models nested inside larger ones, or by coupling models for different processes wit appropriate functions. Flows of matter and energy at a leaf or canopy scale can be simulated by process models and combined with gap or Markovian models at a landscape scale. Flow models can also be combined with demographic models and these can be coupled to climatic, land use or other models, looking for a double approach bottom-up and up-down.

Fire and vegetation fire responses: recent advances in Catalonia

Fire is probably the disturbance with the highest potential to change vegetation and forests in the Mediterranean countries, because fire regime is changed fast by the increasing human impact and because climate change affects in many ways the probabilities of fire ignition and propagation (Piñol *et*

al., 1998). As a result, many efforts are directed to fire modelling. This topic covers such a number of aspects that can not be summarized here. I will comment briefly just some advances done with a major activity of our teams, at CREAF.

Some models address just to the process of burning. The prediction of a fire trail is practically impossible, because too many variables can influence fire propagation. Simple models will be more useful. One has been developed by Piñol *et al.* (2005). In it, fire and some basic management techniques are included in a simple vegetation dynamics model, but there is no detailed description of the real landscape. The main objective is to summarize the fire regime of any region. The region is represented by a 316 × 316 units or pixels intended to represent a 1ha of size in a real landscape. Topography and wind are assumed constants. Potential ignitability and burning intensity increase linearly with the age after last fire until reaching a level where they become constants. The time step is a year. Year climate conditions are obtained from a normal distribution and meteorology affects ignitability and burning intensity. Thus, real potential ignitability will propagate or not after a number of conditions that include random processes. The fire will be extinguished or not depending on the extinction capacity and a random factor. Prescribed fires in randomly distributed grid units can be added to the model. This model has been used to try to respond a relevant question for management and has been calibrated in Spain (Tarragona) and Portugal (Coimbra).

The main debate about fire is about which factor, fuel accumulation or meteorological variability, is the fundamental control of the occurrence of large fires in the Mediterranean-type ecosystems, because if the fuel accumulation is in control than fire-extinction strategies will enhance the occurrence of large fires. A conclusion of the model is that annual area burnt is fairly constant for different fire-fighting capacities, but increasing fire-fighting capacities produces a slightly higher proportion of large fires. If prescribed fires are used, total annual burnt area is also constant, but the proportion of large fires greatly decreases with an increase of prescribed burning.

A very different approach consists in to associate fire and landscape dynamics. Lloret *et al.* (2003) analysed both and related them with the expansion of *Ampelodesmos mauritanica* in the Garraf shrublands. Their work consisted in field surveys in three areas with none, one or two fires during the last 31 years, and in modelling exercises. Succession was simulated using the FATE method (Moore & Noble 1990). FATE (Functional Attributes in Terrestrial Ecosystems) is a deterministic qualitative vegetation model based on the vital attributes approach (Noble and Slatyer 1980). It simulates cohorts of plants that pass through a series of discrete stages, propagules, germinants, immature plants and mature plants, and it is not spatially explicit. The main conclusion of the study is that high fire recurrences permit an increase of the resprouter *A. mauritanica* and a decrease in *Pinus,* whereas the seeders *Rosmarinus* and *Cistus* achieved maximum abundances at intermediate fire recurrences. Recently, the model has been made spatially explicit (Grigulis *et al.,* in press) using the landscape simulation platform LAMOS (Lavorel *et al.,* 2000). In that case, the authors assumed a homogenous substrate and a flat topography for a total area of 100 ha, with the hypothesis that life histories and ecosystem effects of the different species were enough to explain the dynamics of invasion through a positive fire feedback loop. In essence, the method simulates fire response, recruitment, and light competition among plant functional types (PFT) as a function of a limited set of life history parameters, or vital attributes. FATE focuses on cohorts within a PFT. Each life-stage has different responses to environmental conditions and to disturbance. To account for these responses FATE is divided into three submodels: life-history, competition and disturbance.

There are many processes that might affect the recruitment of a plant species, from seed production, dispersal and predation, to seed germination and seedling establishment, and most of them show large spatial and temporal variations (e.g., Lloret 1998, Picó and Retana 2002, Retana *et al.,* 2002, Ordóñez and Retana 2004). For this reason, most forest models consider recruitment as a stochastic process not quantitatively linked to the adults present (Ribbens *et al.,* 1994), or only model one or few of these processes (e.g., Greene and Johnson, 1996), because the empirical data to parameterize them are not available. This is the reason why Ordóñez (2004) has developed a simulation model that predicts the recruitment from unburned edges in large burned areas previously covered by *Pinus nigra*, a species that usually does not regenerate fast after fire. The model includes independent stochastic processes, as cone and seed

production and predation and seedling establishment, and many of the processes involved in the recruitment of a tree species. Results suggest that the presence of *P. nigra* after large fires decreases drastically because seedlings germinate and establish mainly at short distances from the margin, giving rise to a dramatic drop in the number of propagules in the majority of the burned area. The model has been validated with field observations and its sensivity tested, giving as a result that the model is highly dependent on dispersion. The number of seedlings close or far from the unburned margin increased with tree density when trees were medium-sized or large, but was almost nil when trees were small. Plots with medium-sized and large trees almost doubled the distance at which seedlings established compared to those with small trees.

To conclude this general overview, I summarize present state of the art by saying that there are good and bad news. The good news are that the use of computer models, long-term observations, inventories designed to include ecological variables, remote sensing and GIS, geostatistics, and the great advances in the understanding of ecophysiological and biogeochemical ecosystem processes, are deeply changing traditional approaches to vegetation and forest dynamics. The bad news that we are in an urgent need of develop the knowledge and to increase the tools to cope with the fast rates of change in the environment, the vegetation cover and land use and the complex processes that link vegetation to atmospheric and climate variables and to disturbance regimes.

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